## MULTIVARIATE ANALYSIS OF THE VEGETATION IN A TWO-DESERT INTERFACE

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ABSTRACT.— This report further describes the distribution and ecological characteristics of the natural vegetation at the Mojave Desert-Great Basin Desert interface. The region studied is one of extraordinary biological interest because of its geographic location straddling the boundaries of two large deserts of the western United States, and because of the kind and manner of its past land use (atmospheric and underground testing of nuclear devices). The present analysis determines the magnitude of variations in the phytosociological structure in this region and evaluates some relationships between its vegetation and environment. Vegetation and soils were sampled in 66 stands representing many possible physiographic variations. Relative density and relative coverage were determined for each perennial species and summed to provide an estimate of its importance value (I.V.). Importance values were used to ordinate stands to provide a synthesis of the phytosociological data and to portray the compositional relationships of species. The results of this study indicate that the area is dominated by several interrelated vegetational groupings. Correlations between the vegetational groups and the different environmental variables indicate that the distributional pattern of the vegetation is controlled largely by soil physical properties, salinity, and fertility levels.

The landscape of the Nevada Test Site is one of the most intensively studied and best understood deserts in the United States. Its potential is unique for studies critical to better understanding of arid lands. Previous phytosociological studies in this area are largely descriptive (Wallace and Romney 1972, Romney et al. 1973, Beatley 1976).

The objective of this study was to use some multivariate methods to analyze sociological relations among plant communities of the natural vegetation on the Nevada Test Site. This study is closely related to that previously carried out by the authors (El-Ghonemy et al. 1980), in which an account is given on the location, physiography, climate, vegetational groupings, and community diversity.

## MATERIALS AND METHODS

Procedural details involving selection of stands and sampling techniques for soil and plants at 66 sites (Table 1) have been reported by Wallace and Romney (1972) and Romney et al. (1973). For treatment of data, one classification and two ordination techniques were used to analyze a data matrix consisting of the importance values for each of the perennial species encountered in each of the stands.

The classification technique involves the unweighted pair-group agglomerative clustering, using arithmetic averages to compute the similarity between a cluster and a stand which is a candidate for entry into a cluster (Sneath and Sokal 1973). The Euclidean distances (Ed) were used as the measure of similarity between stands.

The first ordination technique is that of Wisconsin (Gray and Curtis 1957) as modified by Beals (1969). The raw data were normalized by row and column, and interstand similarities were calculated using the formula  $2w \div (a + b)$ , where w represents the sum of the smaller values for common species; a and b represent the sum of all species in stands A and B, respectively. The maximum dissimilarity value was set equal to the maximum similarity value found in the similarity matrix. Ten percent of the i'th axis was searched to locate the second end stand for the (i + 1)'th axis.

The second ordination technique involves principal component analysis of the matrix of interstand correlation coefficients (Sneath and Sokal 1973). Eigenvectors (normalized to the eigenvalues) were not rotated.

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## RESULTS

## 1. Classification of the Vegetation Data

(a) The clustering units.- The program cluster was used and Ed was selected as a measure of similarity. It should be mentioned that with this method of classification the stands are clustered into cells regardless of whether they form discrete groups in nature or whether they are merely parts of a continuum. The dendrogram shown in Figure 1 is derived from this cluster analysis. Because the paired and grouped stand clusters in the dendrogram result in linkages at various levels of similarity, an ecologically meaningful classification is not automatically indicated. Classification can be obtained, however, by setting more or less arbitrary threshold values. Threshold values used were set at 10, 15, 20, and 29 Ed. These are indicated by horizontal dash lines on the dendrogram.

At Threshold Line 4 there are three main clusters. Cluster 1 links together 58 stands (1 through 62) at Ed distance of about 28. Cluster II links together 5 stands (21 through 24) at Ed of 20. Cluster III links together stands 33, 39, and 35 at Ed of about 16.

At Threshold Line 3 clusters II and III remained unaltered, but cluster I became distinguishable as three subclusters: subcluster IA that links together 50 stands (1 through 65), subcluster IB that links together stands 54 and 62. At this level of similarity stands 19, 31, and 11 became so dissimilar to other stands that they remain rather isolated.

At Threshold Line 2 the subcluster IA became distinguishable as five vegetational groupings. The first grouping, IAa, links together 11 stands (3 through 34). The second grouping, IAb, links together 12 stands (6 through 51) at Ed of 12. The third grouping, IAc, links 8 stands (4 through 15) at Ed of about 14. The fourth grouping, IAd, links 6 stands (12 through 48) at Ed of about 14.5. The fifth grouping, IAe, links together stands 50, 64, 66, and 65 at Ed of about 16. At this level of similarity many individual stands or

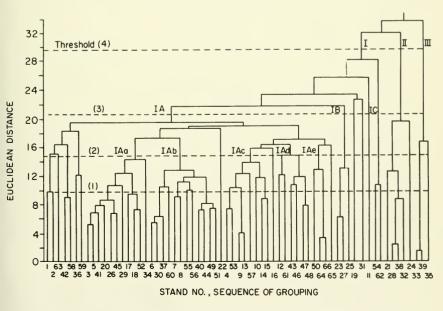


Fig. 1. Dendrogram resulting from the application of the agglomerative clustering analysis. The dotted lines denote the levels at which the dendrogram yields different vegetational groupings.

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TABLE 1. Relative dominance of major species in each of the 66 stands (those 2 percent or more for a given stand) (see Table 2 for plant abbreviations.)

tand 0.	45	Aco	Ef	Lt	Ys	La	Ms	٩d	Gs	Кр	Cl	Pfr	En	
													Mercury	Valle
1	2.3	14.4	25.4 7.1	31.1 37.6	25.4	10.3	13.8							
3			6.3	46.0	14.9	15.4	10.0	8.8	3.6	-3.6				
	14.4		2.3	21.9	6.7	19.4		11.1	13.0		5.9			
			0.0	42.0	13.7	15.3		12.9	2.2	5.9		-3.4	4.5	
	2.5			46.7		2.3		34.6		10.1			2.4	
				9.2		2.5		71.9		16.3				
			10.8	26.7				.38.2		7.4			15.0	
	23.1			22.5		14.9			-31.6					
	6.8			36.8				3.4	40.0					
						10.9								
						9.8			6.0	2.6		22.6	16.1	
	31.6			13.3		15.8			23.1		5.3		5.0	
													Frenchm	
	6.3			20.3		8.5		-3.4	16.8		5.6			.30
	3.2			33.8		20.9		4.8	25.3		11.8			
	3.7							15.1	4.9		24.2			11
	2.3			84.3					4.9		6.4			
				81.1		8.1		2.3	4.4					
				62.3		7.0		3.5	7.8					17
				62.3		4.1		3.5	1.0					30
				20.4		3.0		7.4		22.3		43.4		
	5.2	4.4		20.4 37.9		5.0		1.4		22.0		10.1		
	3.2	-4.4		31.9										
		0.4	4.5	4.4			5.8	9.7		6.3		2.9		
		10.0	1.0	53.9		25.0	0.0	5.1		15.3		2.0		
	2.5	7.4		53.6		20.00				10.0				
	2.0	1.1		5.9.0										
		4.6		50.7				2.1		9.1		5.3	5.7	
	2.8			71.7				15.5		6.9	2.5			
		39.4		54.0							5.4			
		31.5												
		100.0												
				91.3										
		65.2						2.0			5.7			
		12.3		6.7				5.9		24.5			47.2	
		3.7		64.6				13.4	3.3		14.0			
		97.6									2.4			
				28.6				22.8	34.1				10.9	
				57.4		14.9		5.9	8.3				11.8	
		2.2		50.3		4.6	29.6	2.3		3.4	2.9			
											2.8		Rock 6.2	Vall 10
		7.6		6.3 11.3		7.5		11.7	20.3 20.0	28.6 7.0	2.8		6.2	16
		1.6		46.3		$\frac{5.8}{27.7}$		31.3 13.6	20.0	8.5			2.1	1
				46.3 15.6		30.0		13.6		23.3			2.1	
				15.6 21.1		30.0 39.0		12.4	14.4	4.2	2.2		10.5	(
				34.5		39.0		6.6	5.4	4.2	2.2		7.5	4
				24.0		31.5 15.4	2.4	22.2	- 0.4 10.8	1.2			11.9	
				8.6		2.1	T	12.5	59.4				5.6	1
				0,0		<i>2</i> .1		12.0)	00.1				0.0	11
													Jacks	ISS Fle
				26.0		21.0		35.9	5.5			2.6	3.3	
				84.1		4.0		11.6						
	14.6			29.6		5.6		13.6	5.7		11.9			1-
				39.5										
	3.6			19.4		1.5	3.9	26.5	2.2	6.0	7.3			
	2.2			3.3			5.4	39.9		12.8			27.9	
	28.7			42.9			2.6		16.2				5.0	
				27.5			26.5			7.0			16.6	
				19.0			19.0		14.5		3.5		43.7	
	16.4			31.3			11.3	37.3			3.2			
														cca Fi
		5.2				12.3							13.0	
						11.7							61	
	11.5	41.4					16.9				6.5			
						17.5			57.0				55	
				18.5		10.5			16.5				17.2	
						23.0			38.9				14.5	

Table I	continue	ed.											
нь	Lf	Sp	Mt	Мр	Та	Ssp	Aca	Asp	Рр	Ls	Cr	Yb	lle
5.9	36.1	50 7											
22.7 2.0	3.4	52.7 5.6	6.5	3.3	2.0								
						4.3							
12.9					3.8		18.6	2.3					
				24.1			60.9		2.0				
							61.5						
	32.3						57.4			52.0			
										36.9 36.3	11.9		
3.3							98.4					17.6	
4.6							68.5						
4.1							7.0 22.7						
							4.4 99.7						

		60.2 29.4 8.2	4.5
		22.0	
3.3 12.1	5.0	34.9 26.7 62.1	
12.1	3.8	14.0	
	3.3	4.9	7.2
		4.9 35.7 9.5	
11.5		9.5	

couples of stands become mostly dissimilar to the well-defined clusters so that they remain isolated (Fig. 1).

Classification at Threshold Line 1 resulted in many fragmentary units of limited generalizable value.

Sociological significance of the vegetation groupings.— For purposes of discussion each of the clusters identified, irrespective of its hierarchal level on the dendrogram, was called a vegetational grouping and named after the most abundant species, that is, the species with the highest average importance value.

Table 2 includes the average importance values for the different species in the various vegetational groupings. Inspection of this table gives the following explanation of the results of the cluster analysis.

Vegetational Grouping IAa-Larrea tridentata (Sesse & Moc. ex DC) Cov.: This grouping is represented by stands from Frenchman Flat (7 stands), Mercury Valley (2), Jackass Flats (1), and Rock Valley (1). The clustering seems to be based on the presence of L. tridentata as a leading dominant in all the stands in the cluster. The average importance value of L. tridentata (Table 2) is 93.4 (out of 200). The associated species are generally of minor importance, except Ambrosia dumosa (A. Gray) Payne (I.V. = 23.8). Stand 36 (Fig. 1), although dominated by L. tridentata (I.V. = 112), is the last to join the cluster. This is primarily due to the presence of Atriplex canescens (Pursh) Nutt. in substantial amounts (I.V. = 55).

Vegetational Grouping IAb-A. dumosa: This cluster does not appear to be a very natural unit, and on the basis of the subleading dominant species there would be grounds for the recognition of three smaller clusters (Fig. 1). The most influential species responsible for the segregation of this vegetational grouping into smaller clusters are L. tridentata (in stands 6, 30, 37), Krameria parvifolia Benth and Coleogyne ramosissima Torr. (in stands 7, 8, 55, 56), Grayia spinosa (Hook.) Moq. (in stands 40, 44, 49, 51), and Oryzopsis hymenoides (Roem. & Schult.) Ricker (in stand 60). The average importance value for A. dumosa in this grouping is 77. Associated species of pronounced significance are L. tridentata (I.V. = 37) and K. parvifolia (I.V. = 29.4).

Vegetational Grouping 1Ad-Transitional: Stands of this grouping also show little resemblance and mostly fuse in pairs above an Ed of about 10. Dominance is shared by many species, among them Lycium andersonii A. Gray (I.V. = 22.2), Ephedra nevadensis S. Wats. (I.V. = 22.1), O. hymenoides (I.V. = 17), and C. ramosissima (I.V. = 15).

Vegetational Grouping IAe–G. spinosa: The relatively high similarity between stands 64 and 68 (Fig. 1) is not only due to the dominance of G. spinosa, but also due to the preponderance of L. tridentata, E. nevadensis, and C. ramosissima. The average importance value of G. spinosa in this grouping is 71, followed by 23 for L. andersonii and 22.5 for C. ramosissima.

Vegetational Grouping IB-Lycium shockleyi A. Gray (L. rickardii) C. H. Mull.: All stands of this cluster are also dominated by L. shockleyi, with an average importance value of 88. Other important species are L. tridentata (I.V. = 35) and Atriplex confertifolia (Torr. & Frem.) S. Wats. (I.V. = 27).

Vegetational Grouping IC-C. ramosissima: All of the five stands representative of this cluster are dominated by A. canescens. Stands 28 and 38, which fuse at very high similarity levels, are overwhelmingly dominated by A. canescens (I.V. = 188 and 185, respectively). The average importance value for A. canescens in this cluster is 150. Species of some importance are Stanleya pinnata (Pursh) Britt. (I.V. = 18) and Lycium pallidum Miers (I.V. = 8.4).

Vegetational Grouping III–A. confertifolia: This is the last cluster to join the dendrogram, and it enters at a very low level of similarity (Ed = about 33). All stands are dominated by A. confertifolia. Stand 33 (I.V. = 200) fuses with 39 (I.V. = 193) at the highest recorded level of similarity (Ed = 0.8). Stand 35, which is also dominated by A. canescens, has a high (45.6) importance value for A. canescens as well as for Ceratoides lanata (Pursh) J. T. Howell (I.V. = 22). This results in its fusion with stands 33 and 39 at a relatively low similarity level (Fig. 1). Other species in this grouping are of little significance.

#### 2. Ordination of the Vegetation Data

(a) Ordination of Stands: According to the Bray and Curtis (1957) technique, the two-dimensional ordination of stands (Fig. 2) has resulted in three distinct hyperspheres which correspond to the vegetation groupings identified at Threshold Line 4 on the dendrogram derived from the cluster analysis and superimposed on the ordination plane. Smaller vegetational groupings identified at higher similarity levels (Threshold 2) are mostly interconnected on the ordination plane (see dashed lines), but are still distinguishable in the form of successive groups of stands segregated along the primary X axis.

In the application of principal component analysis (PCA), five components or axes were extracted that account for 65.3 percent of the total variation (Table 3). Plotting of stand scores (Figs. 3 and 4) on the two axes that showed a greater number of significant corre-

TABLE 2. Average importance values for 35 perennial species in the different vegetational groupings (see Fig. 1).

	Lt (IAa)	Ad (IAb)	As (IAc)	Trans <sup>e</sup> (IAd)	Gs (IAe)	Ls (IB)	Cr (IC)	Aca (II)	Aco (III)
T T T									(111)
Larrea tridentata (Lt)°°	93.4	39.2	30.3	41.8	13.5	38	24.0	-	_
Ambrosia dumosa (Ad)	23.8	77.4	15.8	14.5	14.0	2	0.3	0.5	1.3
Oryzopsis hymenoides (Oh) Ceratoides lanata (Cl)	7.0	7.2	10.1	1.0	3.3	3	_	3.1	2.2
	5.0	3.6	23.7	4.0	2.9	-	0.6	1.0	9.3
Sphaeralcea ambigua (Sa)	2.6	1.2	2.0	1.2	-	2	3.3	2.2	-
Lycium andersonii (La)	16.0	5.3	17.4	38.0	23.0	_	11.0	2.4	
Mirabilis pudica (Mp)	0.1	_	_	2.6		1	_	3.0	_
Hymenoclea salsola (Hs)	0.8	_	2.5	11.2	5.1	î	8.1		2.7
Acamptopappus shockleyi (As)	6.8	7.4	44.9	_	_	21	_	_	
Ephedra funerea (Ef)	2.0	1.1	2.3	_	_	4	_	_	_
,,									
Psorothamnus fremontii (Pfr)	5.6	0.7	0.1	9.2	_	_	_	_	_
Krameria parvifolia (Kp)	5.2	29.4	3.9	22.2	_	5	_	_	-
Yucca schidigera (Ys)	3.3	_	0.8		_		_	-	_
Yucca brevifolia (Yb)	1.8	_	_	5.0	_	2	_	_	_
Lycium pallidum (Lp)	3.1	3.1	9.0	10.3	_	_	-	8.4	_
Lepidium fremontii (Lf)	0.3	0.4	0.5	1.9	_	_	_	-	_
Ephedra nevadensis (En)	5.5	6.8	3.9	22.1	20.0	_	6.3	_	_
Menodora spinescens (Ms)	-	1.3	0.5	0.5	-	4	0.8	-	_
Grayia spinosa (Gs)	11.1	10.3	37.4	17.0	71.5		-	0.9	0.6
Coleogyne ramosissima (Cr)		4.5	-	15.0	22.5	6	137.0	-	-
Machaeranthera tortifolia (Mt)		1.0	0.6	5.1			2.4		
Cactus spp. (Ca)	1.0	1.0	0.6	0.1	0.2	_	2.4 0.4	-	-
Stipa speciosa (Ssp)	1.0	_	0.9	_	22.0		0.4	-	_
Tetradymia axillaris (Ta)		_	1.0	0.3	0.4	-	3.3	_	_
Atriplex confertifolia (Aco)	_	1.0	1.0	0.5	0.4	23	0.4	12.8	188.0
implex conferngona (.xco)		1.0	_	-	_	20	0.4	12.0	100.0
Atriplex canescens (Aca)	5.0	1.0	_	-	_	_	_	150.0	15.0
Stanleya pinnata (Sp)	-	_	-	0.3	_	_	_	18.0	_
Hilaria rigida (Hr)	-	0.1	0.3	_	_	_	_	_	_
Lycium shockleyi (Ls)	—	_	_	_	_	88	_	_	_
Artemisia spinescens (Asp)	-	-	0.6	_	_	_	_	_	_
Prunus fasciculata (Pf)	_	-	-	-	-	-	-	-	-
Salazaria mexicana (Sm)	-	-	-	-		1	_	-	-
Thannosma montana (Tm)	0.2	-	-	-	-	-	-	_	-
Haplopappus cooperi (Hc)		_	0.6		-	-	-	-	-
Psorothamnus polyadenius (Pp)	1.0	_	-	_		-	-	-	-

<sup>\*</sup>Transitional

\*\*Letters in parentheses indicate abbreviations for species' names. Table headings correspond to these abbreviations.

lations with environmental variables, viz., Axes I and III, show that the application of PCA technique has resulted in much better segregation of stands into groups comparable with those derived from the clustering technique at Threshold Line 2 on the dendrogram.

The two vegetation groupings of A. canescens and A. confertifolia are separated at the negative side of the first axis. Separation of the two groupings from one another is affected by the third axis. Stand 35, which joins the *A. confertifolia* grouping at a relatively low level of similarity (Fig. 1), appears on the ordination plane to be more associated with the *A. canescens* grouping. The groupings of *L. tridentata* and *A. dumosa*, which have more or less overlapping scores on the first axis, are

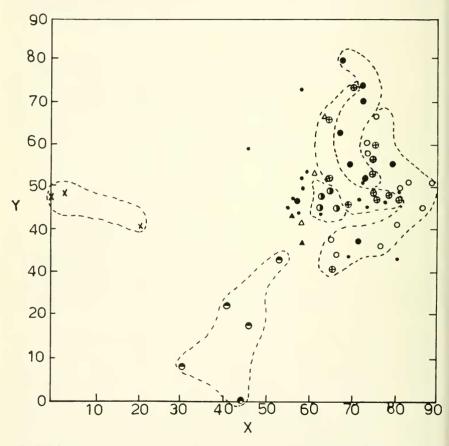


Fig. 2. Ordination of the stands on the first axes derived from the Wisconsin ordination (Bray & Curtis) technique. The classification of stands according to the cluster analysis has been superimposed on the ordination diagram. Dashed lines connect some of the vegetational groupings. Empty circles are stands of *L. tridentata* (IAa), crossed circles are stands of *A. dumosa* (IAb), vertically half-blocked circles are stands of *G. spinosa* (IAe), horizontally half-blocked circles are stands of *A. canescens* (II), large blocked circles are stands of *A. shockleyi* IAe), blocked triangles are stands of *C. ramosissima* (IC), empty triangles are stands of *L. shockleyi* (IB), crosses are stands of *A. confertifolia* (III), and small blocked circles are transitional stands (OAd).

clearly separated on the third axis. Along this axis A. dumosa scores positive values, but those of L. tridentata are negative. Along the first axis the groupings of L. tridentata, A. shockleyi, L. shockleyi, and C. ramosissima are also separated from one another. The grouping of G. spinosa is primarily separated from other groupings along the third axis. It is also apparent (Fig. 4) that the groupings of L. shockleyi and C. ramosissima occupy a more or less central position between other groupings.

(b) Behavior of species along the environmental gradients: The behavioral pattern of eight common species as expressed by their importance value is represented separately on the ordination derived from the first and third axes of the PCA (Fig. 5:A-H). Larrea tridentata and A. dumosa attain their high importance values at the high and medium positions of the positive side of the axis. Along the third axis the two species behave rather differently: the high values of A. dumosa are on the positive side and the high values of L. tridentata are on the negative side. Grayia spinosa and L. andersonii also exhibit definite patterns, with their high importance values at the medium position on

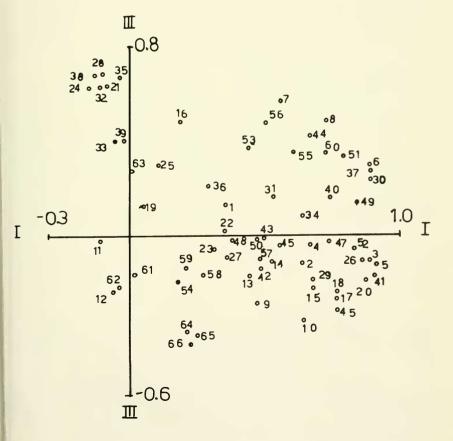


Fig. 3. Plotting of stands on axes I and III from the principal component analysis (PCA).

the first axis. Acamptopappus shockleyi shows its high values at medium to lower positions on the positive side of the first axis. On the third axis most of the high values are on the negative side. More definite patterns are those of *A. canescens* and *C. ramosissima*. They have attained their high importance values at the extreme positive and the extreme negative end of the third axis, respectively. *Atriplex confertifolia* attained its high importance values at the central positions with regard to the positive side of the third axis.

(c) Ecological significance of phytosociological gradients: Simple correlation coefficients between the phytosociological gradients represented by the five axes extracted from the PCA and the various environmental variables are given in Table 3. Most of the correlations are extremely low. The lowest negative correlation (-0.39) is that between the first axis and field capacity for water relations in soil. This axis is also significantly correlated with both sodium (negative) and iron (positive). Axis 2 shows no significant correlations with any of the variables studied. Axis 3 shows significant correlations and most of the variables correlated significantly with the first axis, but with opposite trends. This axis also shows significant correlations with both potassium (positive) and nitrogen (negative). Axis 4 shows significant positive correlations with electrical conductivity and potassium, and axis 5 shows significant positive correlations with soil moisture retention capacity, electrical conductivity, calcium, magnesium, copper, and nitrogen.

It is apparent from these correlation studies that the segregation of the vegetation cover into distinct groupings on the ordination plane is largely attributed to variations in soil properties. The vegetational grouping of A. canescens and A. confertifolia occupy sites poor in phosphorus, organic matter, and nitrogen, but rich in sodium, potassium, copper, and percent of clay. The grouping of A. dumosa reflects sites rich in phosphorus, iron, and to some extent in sodium, but poor in nitrogen. The Gravia spinosa grouping occupies sites decidedly poor in sodium, potassium, and fine particles, but rich in nitrogen and iron. The groupings of L. shockleyi and C. ramosissima occupy sites with more or less intermediate soil characteristics.

(d) Correlation among species and species ordination: The spatial pattern of one species may be modified by another. This leads to the question of interspecific correlation. The causes of these correlations are, however, varied. The most common cause is, no doubt, the mutual response to varying environments. There also are interactions between species that do not involve independent environmental factors (allelopathic effect, competition, or amelioration or degradation of environmental conditions). It is, however, difficult to reach firm conclusions as to the cause of cor-

TABLE 3. Simple linear correlation coefficients (r) between five principal components and the various environmental parameters\*

Parameter PCA axes	Proportion of total variance Percent	Accumulated variance Percent	F. Cap.	pH	EC	Lime Percent
1	31.1	31.1	-0.39°°°	-0.13	0.04	-0.20
2	11.1	42.2	0.05	0.21	0.08	0.21
3	8.1	50.3	0.10	0.07	0.09	-0.06
4	7.9	58.2	0.22	-0.03	0.27°	-0.07
5	7.1	65.3	0.38 ***	0.07	0.31°°	0.08

\*A single asterisk denotes a significant correlation at 5 percent probability level. Double and triple asterisks denote a significant correlation at 1 percent and 0.1 percent probability levels.

F. Cap. is water retention at field capacity.

EC is electrical conductivity.

Cations are exchangeable

Fe, Zn, and Cu are from 0.005 M DTPA extract.

N is total soil nitrogen.

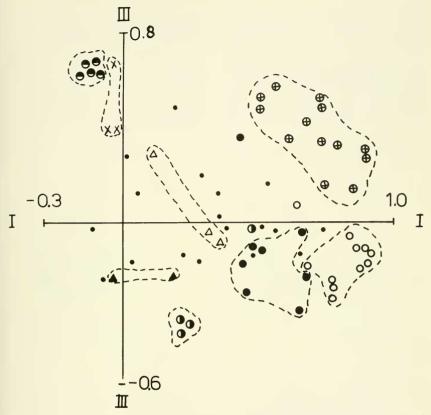


Fig. 4. Ordination of stands on axes I and III from the principal component analysis. The classification of stands according to the agglomerative clustering analysis has been superimposed on the ordination diagram. For identification of groupings see Fig. 2.

Table 3 continued.

Na	К	Ca płus Mg	Na	Р	Fe	Zn	Cu	N	
	me/100 g		%	µg∕g	$\mu$ g	g/g DTPA	ext.	%	Elevation
-0.34 ***	-0.19	-0.17	-0.30°°	-0.32°°°	0.31°°	-0.06	-0.28°	0.10	0.18
0.12	0.08	-0.10	0.15	-0.17	-0.21	0.05	-0.22	-0.13	0.03
0.35°°	0.28°	-0.14	0.34°°°	-0.16	-0.37°°°	-0.21	-0.15	-0.31°°	-0.10
0.23	0.34°°°	0.17	0.17	0.05	0.07	0.14	-0.21	-0.10	-0.1
-0.12	0.21	0.25°	-0.20	0.18	0.11	0.13	0.31 **	0.27°	0.03

relations by simply observing the spatial distribution of the two species in nature; however, if neither species separately shows any patterning but the two random distributions are coincidental (or countercoincidental), a direct relationship between the species seems the most likely explanation (Goodall 1970).

In Table 4 a partial simple linear correlation matrix is given for 35 common species showing the positive and negative relationships present. The species constellation based on correlation values is illustrated in the form of a three-dimensional diagram in Figure 6. The components involved in the construction of this diagram were extracted using the principal component analysis of the matrix of interspecific coefficients (Sneath and Sokal 1973). Five groupings of species are apparent—a central group and four peripherals. The arrangement of species in this diagram

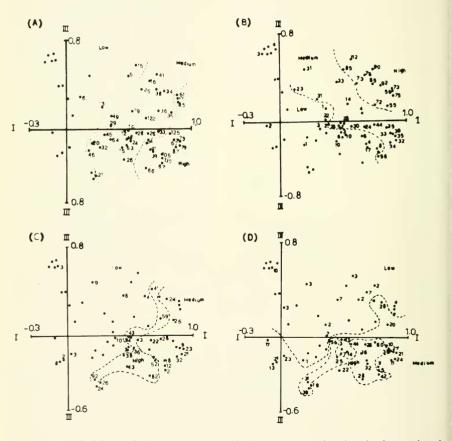


Fig. 5. (A-H). The behavior of eight species as expressed by their importance values along the phytosociological gradients expressed by the first and third axes of the principal component analysis. The importance value for each are superimposed upon a common ordination plane. High, medium, and low values are indicated where appropriate. A is *L. tridentata*, B is *A. dumosa*, C is *G. spinosa*, D is *L. andersonii*, E is *A. shockleyi*, F is *A. canescens*, G is *C. ramosissima*, and H is *A. confertifolia*.

reflects positive correlations in the main, the general position of each grouping of species being related to the negative correlations also present. The following are the five groups identified:

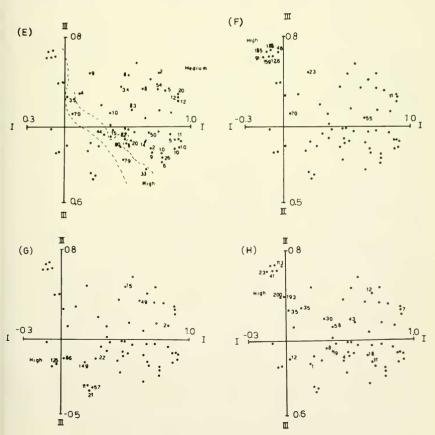
Group 1 (upper left-hand side of the diagram): Grayia spinosa, L. andersonii, L. pallidum, Stipa speciosa.

Group 2 (lower left-hand side): Ambrosia dumosa, Hilaria rigida (Thurb.) Benth. ex Scribn., Yucca schidigera Roezl ex Ortgies, Ephedra funerea Cov. & Mort., Salazaria mexicana Torr., E. nevadensis, K. parvifolia. Group 3 (upper right-hand side): Hymenoclea salsola Torr. & Gray, Tetradymia axillaris A. Nels., A. shockleyi, Machaeranthera tortifolia A. Gray, Sphaeralcea ambigua A. Gray.

Group 4 (lower right-hand side): Yucca brevifolia Engelm. in Wats., Thamnosma montana Torr. & Frem., Psorothamnus fremontii (Torr.) Barneby, Prunus fasciculata (Torr.) A. Gray, Cactus species.

Group 5 (central): Psorothamnus polyadenius (Torr.) Rydb., A. canescens, A. confertifolia, Mirabilis pudica Barneby, O. hyme-

Fig. 5 continued.



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noides, Mendora spinescens A. Gray, L. tridentata, S. pinnata, P. fremontii, Haplopappus cooperi (A. Gray) Hall, L. shockleyi, C. lanata, Artemisia spinescens D. C. Eat., C. ramosissima.

It is equally clear that none of these five groups is an isolated entity; each is linked to the adjacent group by correlations of different magnitude between member species of the representative groups or through intermediate species.

The deduction that these correlated groups of species represent significant communities in nature may not necessarily hold. The very obvious group on the lower right-hand side of the diagram (Group 4) includes species of minor significance in vegetation structure (very low importance values), and consequently such a group is not detectable in nature. On the other hand, group 1, dominated by *G. spinosa*, *L. andersonii*, *S. speciosa*, and *C. ramosissima*, is well defined in nature and floristically structurally comparable with the *G. spinosa* grouping previously defined by stand classification and ordination techniques.

## DISCUSSION

The data obtained by measuring the amount of a species in each of n stands can be represented by a scatter diagram of n

TABLE 4. Part of simple linear correlation matrix for 35 perennial specimens for the northern Mojave Desert showing positive and negative species' relationships.

Acamptopappus shockleyi (As)	+ 0.34°°°Oh, +0.29°Mp
Atriplex confertifolia (Aco)	-0.28°La
Ephedra funerea (Ef)	$+0.75$ Ys, $+0.29^{\circ}$ Hr
Ceratoides lanata (Cl)	+ 0.27°Lp, + 0.35°°°Ta, + 0.63°°°Asp
Ambrosia dumosa (Ad)	$+0.26 + Kp, +0.28^{\circ}Hr$
Krameria parvifolia (Kp)	$+0.50^{\circ\circ} {}^{\circ}En$ , $+0.27^{\circ}Pfr$ , $+0.25^{\circ}Ca$ , $+0.29^{\circ}Pf$ , $+0.26^{\circ}Ad$
Larrea tridentata (Lt)	-0.27°Ta, -0.25°Aca, +0.36°°°Pp
Lycium andersonii (La)	+ 0.38°°°Gs, + 0.25°Oh, -0.60°°°Pp, -0.28°Aco
Menodora spinescens (Ms)	
Yucca schidigera (Ys)	+ 0.75°°°Ef
Sphaeralcea ambigua (Sa)	$+0.33^{\circ\circ\circ}Mt_{s} + 0.25^{\circ}Hs$
Ephedra nevadensis (En)	+0.50 ° ° Gs
Grayia spinosa (Gs)	$+0.33^{\circ\circ} Ssp. +0.38^{\circ\circ} La$
Lepidium fremontii (Lf)	$+0.68^{\circ\circ\circ}Sp$
Oryzopsis hymenoides (Oh)	$+0.25^{\circ}$ La, $+0.62^{\circ\circ\circ}$ Mp, $+0.34^{\circ\circ\circ}$ As
Machaeranthera tortifolia (Mt)	+ 0.33°°°Sa, + 0.41°°°Pfr, + 0.75°°°Hs
Psorothamnus fremontii (Pfr)	+0.27 Kp, + 0.41°°°Mt, +0.33 Hs, +0.63°°°Ca, +0.82°°°Pf,
· · · · · · · · · · · · · · · · · · ·	+ 0.27°Tm
Coleogyne ramosissima (Cr)	$+0.32^{\circ\circ\circ}Ta_{\circ}+0.25^{\circ}Ssp$
Lycium pallidum (Lp)	+ 0.27°Cl
Hilaria rigida (Hr)	+ 0.29°Ef, + 0.28°Ad
Hymenoclea salsola (Hs)	+0.25°Sa, +0.75°°°Mt, +0.33 Pfr, +0.48°°°Ta, +0.33°°°Ta
Stanleya pinnata (Sp)	+0.68°°°Lt
Stipa speciosa (Ssp)	+0.33°°°Gs, +0.25°Cr
Tetradymia axillaris (Ta)	+0.35°°°Cl, -0.27°Lt, +0.32 Cr, +0.48°°°11s, +0.61°°°Asp
Mirabilis pudica (Mp)	$+0.29^{\circ}$ As, $+0.62^{\circ\circ\circ}$ Ob
Atriplex canescens (Aca)	-0.25°Lt
Artemisia spinescens (Asp)	+ 0.63°°°Cl, + 0.33°°°Hs, + 0.61°°°Ta
Psorothamnus polyadenius (Pp)	+ 0.36°°°Lt
Cactus sp. (Ca)	+0.25°Kp, +0.63°°°Pfr, +0.53°°°Pf, +0.45°°°Yb, +0.72°°Tm
Prunus fasciculata (Pf)	$+0.29^{\circ}$ Kp, $+0.82^{\circ}$ °Pf, $+0.53^{\circ}$ °Ca
Lycium shockleyi (Ls)	+ 0.35°°°Sm
Yucca brevifolia (Yb)	+ 0.45°°°Ca, + 0.51°°°Tm
Salazaria mexicana (Sm)	$+0.35^{\circ\circ\circ}Ls, +0.51^{\circ\circ\circ}Tm$
Thamnosma montana (Tm)	$+0.27^{\circ}$ Pfr, $+0.72^{\circ\circ\circ}$ Ca, $+0.51^{\circ\circ\circ}$ Yb
Haplopappus cooperi (He)	

\*Denotes a correlation at 5 percent probability level, \*\* at 1 percent probability, and \*\*\* at 0.1 percent probability.

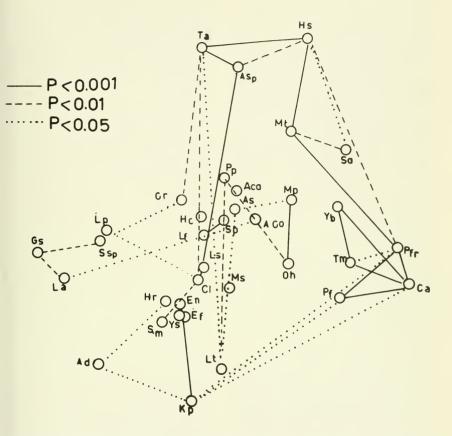


Fig. 6. Special ordination on the first three axes derived from the principal component analysis. Species showing positive correlations are interconnected. Letters beside each circle indicate abbreviations for species' names.

1. As	= Acamptopappus shockleyi	18.	Cr	=	Coleogyne ramosissima
2. Aco	= Atriplex confertifolia	19.	Lp	=	Lycium pallidum
3. Ef	= Ephedra funerea	20.	Hs	=	Hymenoclea salsola
4. Cl	= Ceratoides lanata	21.	Hr	=	Hilaria rigida
5. Ad	= Ambrosia dumosa	22.	Sp	=	Stanleya pinnata
6. Kp	= Krameria parvifolia	23.	Мp	=	Mirabilis pudica
7. Lt	= Larrea tridentata	24.	Ta	=	Tetradymia axillaris
8. La	= Lycium andersonii	25.	Ssp	=	Stipa speciosa
9. Ys	= Yueca schidigera	26.	Aca	=	Atriplex canescens
10. Ms	= Mendora spinescens	27.	Asp	=	Artemisia spinescens
11. Sa	= Sphaeralcea ambigua	28.	Pp	=	Psorothamnus polydenius
12. En	= Ephedra nevadensis	29.	Ca	=	Cactus sp.
13. Gs	= Grayia spinosa	30.	Pf	=	Prunus fasciculata
14. Lf	= Lepidium fremontii	31.	Ls	=	Lycium shockleyi
15. Oh	= Oryzopsis hymenoides	32.	Sm	=	Salazaria mexicana
16. Mt	= Machaeranthera tortifolia	33.	Yb	=	Yucca brevifolia
17. Pfr	= Psorothamnus fremontii	34.	Hc	=	Haplopappus cooperi

points in an s-dimensional coordinate frame. Classification consists of subdividing the swarm of points into a number of disjointed sets. If the points chance to fall into several compact, widely separated groups, no difficulty arises and formal rules for effecting a classification are scarcely needed. According to Pielou (1969) this ideal result is rarely obtained when vegetation is randomly sampled. More often than not, the points representing the stands are diffusely scattered and any

classification procedure is largely arbitrary. A way out of this difficulty is to ordinate the stands rather than to classify them. The purpose as in classification is still to simplify and condense the mass of raw data yielded by vegetation sampling in the hope that relationships among the plant species, and between them and the environmental variables, will be manifested.

Ordination consists of plotting n stands in a space of fewer than s dimensions in such a way that none of the important features of the original s-dimensional pattern is lost. Ordination has two great advantages over classification. It obviates the necessity for setting up arbitrary criteria for defining the classes, and there is no need to assume that distinct classes, if there are any, are hierarchically related. However, the compatability of the two approaches, viz., the classification and the ordination techniques, was pointed out by Anderson (1965) and Goodall (1970), and in recent years it has become more common for classification and ordination to be used on the same data (Gray and Bunce 1972, Williams and Walker 1974, Ayyad and El-Ghonemy 1976).

The importance of the study area from the phytogeographical point of view may be due to its position straddling the boundaries of the Great Basin to the north and the Mojave Desert to the south. The behavior of the biotic communities of the Mojave Desert in general, or in some of its sectors, has attracted the attention of many biologists. Shreve and Wiggins (1964) have described the Mojave Desert as showing its most distinctive development between 600 and 1200 m elevation (2000–4000 ft.). When it is followed thence toward the northeast or southeast, it loses some of its characteristic vegetational features and much of its distinctive flora. The basic structure of the vegetation throughout the Mojave Desert is open stands of *L. tridentata* and *A. dumosa*. On the western edge the plants are joined and to some extent replaced by *A. tridentata*, *G. spinosa*, *T. axillaris*, and other perennials; and at high elevations on the north, *C. ramosissima*, *G. spinosa* are dominant.

In the northern sector of the Mojave Desert, particularly in the Nevada Test Site and its surroundings, phytosociological studies have been carried out by many authors. Among these are Beatley (1963, 1969, 1974, 1975, 1976), Allred et al. (1963), Rickard and Beatley (1965), Brown and Mason (1968), Wallace and Romney (1972), Romney et al. (1973), Tueller et al. (1974), and El-Ghonemy et al. (this volume). In these studies some of the vegetational units have been identified and named by various terms as communities. associations, types, subtypes, and vegetational groupings. In the most recent work by El-Ghonemy et al. (1980) the correlation between the various vegetational groupings identified and the environmental variables have been demonstrated, as well as the vegetation diversity and the successional trends among the different groupings.

In the present study the application of the agglomerative clustering technique has proved useful in classifying stands into several vegetational groupings. However, most of these groupings are not distinct. The members of each pair of groupings are, in most cases, linked together by having one or more of the dominant species in common. This, as Goodall (1954) mentioned, does not preclude the possibility of the classification for particular ends, but it is generally more appropriate to ordinate stands.

In the present study the application of both Wisconsin and PCA ordination techniques emphasizes this idea and indicates that the vegetational groupings yielded by the clustering technique are generally interconnected. However, the PCA technique has proved more efficient in segregating stands in a manner more or less similar to that achieved by the clustering approach. The better segregation of stands along the PCA ordination plan makes the description and correlation of the vegetational grouping more efficient.

The vegetational groupings identified in the study area are more or less similar to those previously identified by El-Ghonemy et al. (this volume) with stands clustered into groupings according to their leading dominant species (i.e., species with highest importance values). Because in the multivariate analysis the similarity between stands involves the use of similarity functions that take into account the whole number of species involved in community structure, the stand's characteristics for a given vegetation unit may not have the same leading dominant species. Consequently, the detailed structure of comparable vegetation groupings derived from the two approaches may not be the same

The spatial arrangement of stands along the different vegetational gradients provides evidence that variations in vegetation composition are expressed by more than one axis of the ordination components. This implies that the distribution of vegetation in the study area is controlled by complexes of interrelated factors. These fall into three main groups. The first group relates to soil fertility, as reflected by the concentrations of phosphorus, nitrogen, potassium, and other nutrient elements. The second complex expresses soil salinity, and the third complex relates to soil texture and water-retention capacity. The role of soil fertility as a factor in the delimitation of the natural plant communities has been stressed by several authors (Beadle 1954, 1962, El-Ghonemy 1966, Avvad and El-Ghonemy 1976).

In the present study the association of certam vegetational groupings, for example, that of A. dumosa, with phosphorus-rich soil, has been demonstrated. The role of total soil salinity or of particular salt has been critically reviewed by Chapman (1960), Gates et al. (1956), Ayyad and El-Ghareeb (1972), and Beatley (1976). The Atriplex communities at the Nevada Test Site have been described by Beatley (1976) as occupying sites at the high end of the soil salt content and fine particle gradients. These results are in full agreement with the results obtained in the present study.

### Conclusions

(1) The application of the multivariate analysis resulted in the segregation of the vegetational cover into more or less distinct groupings.

(2) The application of the principal component analysis for the ordination of the vegetation data resulted in the segregation of stands into more or less distinct sets, comparable in structure to the vegetation groupings derived from the cluster analysis.

(3) The physical and chemical properties of the soil play a definite role in the delineation of the vegetational groupings.

(4) The ordination of species scores may result in groupings of correlated species that could be floristically different from those obtained if ordination is based on stand scores.

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